

Pollen Loads Collected from Large Insects in Australian Subtropical Rainforests

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Pollen loads on insects >9 mm in length, collected principally from the flowers of subtropical rainforest trees, were examined. Primary sites of pollen lodgement on the integument of approximately 60 species of Coleoptera, Diptera and Hymenoptera (Icheumonoidea, Sphecoidea, Vespoidea) were recorded. Hooked setae were recorded for the first time from the beetle genus *Cacochroa* (Cetoniinae-Scarabaeidae).

Although most insects carried mixed pollen loads the low incidence or absence of pollen from non-conspecific plant taxa ('foreign' pollen) indicated temporal foraging constancy for some species. Insects foraging on Myrtaceae generally carried large pollen loads with little or no foreign pollen. Wasps exhibited considerable variation in the amount of pollen carried. Beetles in the families Buprestidae, Cerambycidae and Scarabaeidae (subfamily Cetoniinae) carried mixed pollen loads, derived from a number of plant taxa, but often in substantial quantities, indicating that Coleoptera are potentially important pollinators of mass-flowering rainforest trees with generalist pollination ecologies.

The foraging behaviour and surface vestiture of individual insect taxa influence pollen loads and sites of pollen deposition on the bodies of insects. All insect taxa examined were observed to make frequent inter-plant movements and undertook relatively long distance inter-plant flights and, consequently, may be important in contributing to outbreeding in fragmented populations of rainforest trees.

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INTRODUCTION

The majority of mass-flowering Australian subtropical rainforest trees appear to be capable of being pollinated by members of a taxonomically diverse assemblage of insects (Williams 1995) and as such are part of the majority of angiosperms which "are generalists in their pollinator requirements" (Ollerton 1996). Most insects visiting Australian subtropical rainforest trees are less than 6 mm in length (Williams 1995), and insects in this size group have been shown to transport pollen and to act as pollinators of a number of Australian tropical and subtropical rainforest plants (Hamilton 1897, House 1985, 1989, Armstrong and Irvine 1989, Williams 1995). Although large ecologically specialised bees are pollinators of some Australian rainforest plants (e.g., Gross 1993), the capacity of ecologically unspecialised larger insects (here arbitrarily characterised as species >9 mm in body length) to transfer pollen in Australian rainforest communities has not been investigated. The decision as to which insects can be considered large is a subjective one but individual insects longer than 9 mm become conspicuous to the casual human observer.

Large insects constituted less than 6 percent of the number of individuals and species of anthophilous insects sampled in Australian subtropical rainforests by Williams 1995. Large insects were absent in many samples from a number of study plants

(Williams 1995). Although larger species make up a small proportion of the flower-visiting fauna, their potential for relatively long-distance inter-plant movements may have important consequences for the reproductive success of disjunct or isolated plants. This may be particularly important for plants possessing small entomophilous flowers as such plants are not regularly visited by bats or birds (Williams 1995) which might otherwise act as long distance pollen vectors. The capacity of a vector to transport pollen is related to body morphology and behavioural patterns (e.g., foraging movements, orientation and contact with floral structures, grooming). The presence of compounds on the exine (e.g., pollenkit) may facilitate adherence to the vector (Faegri *et al.* 1992) but the role of exine sculpture in facilitating pollen transport is unclear (Williams and Adam in press).

Historically, bees (Apoidea) and Syrphidae (Diptera) have been considered as more efficient and specialised collectors of pollen and, consequently, pollinators of flowering plants, than other insects (see Holloway 1976, Armstrong 1979, Roubik 1989, Williams and Adam 1994). The foraging behaviour of eusocial Apidae is well documented (Faegri and van der Pijl 1979, Appanah 1982, Appanah, Willenstein and Marshall 1986, Adam, Fisher and Anderson 1987, Bernhardt and Thien 1987, McAlpine 1988, Bertin 1989, Roubik 1989, Williams and Adam 1994, 1997) but the pollination contributions of other bee families are varied and some groups, for example the Colletidae, may contribute little to reproductive success in plants (see Armstrong 1979, Faegri and van der Pijl 1979, Steiner 1985, Bernhardt and Thien 1987, Williams and Adam 1994). Proenca and Gibbs (1994), however, record pollination of the tree *Siphoneugenia densiflora* Berg (Myrtaceae), in a Brazilian savannah woodland, by the colletid *Ptiloglossa* sp.. Numerous species of aculeate or 'higher' wasps (Vespoidea, Sphecoidea) visit some rainforest plants (Williams and Adam 1995) but their role in pollination has been little investigated.

Although a number of beetle families possess dense or long vestiture (Crowson 1981) Coleoptera have been regarded as 'smooth-bodied' and not likely to be effective pollinators (Percival 1965, Ashton 1969, Armstrong 1979, Archibold 1995). Archibold (1995), for example, citing Faegri and van der Pijl (1979), stated that "Pollen does not readily adhere to the smooth bodies of beetles and their clumsy action usually restricts them to open, bowl-shaped blossoms which offer little reward of nectar or pollen".

Increased surface vestiture, palynophilic (pollen-collecting) setae and frontoventrally placed pollen retaining punctation and foveae, and possibly medial pits and grooves on the disc of the head and elongated mouthparts (as in the *Castiarina* 'producta' spp. group of Coleoptera-Buprestidae), are considered derived apomorphic characters in anthophilous Coleoptera (Holloway 1976, Gardner 1989). Such pollen retaining structures in various pollinivorous Coleoptera may have evolved as food collecting surfaces (Crowson 1981), but may also permit transport of pollen between plants so that insects possessing these structures have the potential to act as pollinators.

Here we present data on pollen loads carried by large anthophilous insects in sub-tropical rainforest remnants and associated ecotones. These data provide:

1. a test of the assertion (Archibold 1995) that superficially smooth integuments render many Coleoptera unlikely pollinators,
2. for those insects carrying pollen, an indication of pollen load capacity and principal sites of pollen deposition on the integument, and
3. an indication of fidelity or constancy of potential vectors to the flower resource (this is only related to the time of sampling and does not indicate how the species may forage at other sites or times).

In addition, we briefly comment on morphological and behavioural factors that influence the amount of pollen carried by individual insects. Our investigation of pollen loads was intended primarily to determine whether individual taxa could potentially act as pollinators, rather than to assess the efficiency of individual taxa as pollinators.

METHODS

As a small component of a study of the pollination ecology of subtropical rainforests (Williams 1995), undertaken in the Manning Valley (approximately 31°52'S, 152°22'E) in coastal northern New South Wales, insects greater than 9 mm in body length were collected to determine their capacity to carry pollen. Latitudes and longitudes of study sites are given in Table 1 and descriptions of the study sites are given in Williams (1993, 1995) and Williams and Adam (1997). The majority of field collections were made between 1990 and 1993. Most specimens collected are lodged in the Australian Museum, Sydney. Insects were collected individually by hand netting as they landed upon, or fed from, flowers. To avoid pollen contamination specimens were placed separately in an insect killing jar primed with ethyl acetate and then stored separately for later examination. Specimens were examined under a binocular microscope. Insects were identified principally by comparison with material held in the Australian Museum, Australian National Insect Collection, CSIRO (Canberra), and the New South Wales Department of Agriculture (Orange).

A summary of the primary pollen deposition sites on the integument of those insects studied which carried pollen is given in the Appendix (insects listed in the Appendix represent the majority of larger-sized native taxa collected during the broader pollination study).

Most pollen was located as aggregations or discrete masses on the insect body. These aggregations were removed with a micropin and embedded in glycerine-safranin gel, to which had been added several drops of phenol to inhibit fungal growth, on a microscope slide. Slides were later examined by light microscope (at X40). The pollen loads examined were rated 'moderate (M)' (>100 grains), 'heavy (H)' (>200 grains) and 'abundant (A)' (>300 grains). Pollen loads <100 grains are given as approximate counts of individual grains (Table 1). Pollen composition was expressed as percent 'home' pollen (House 1985); i.e. pollen conspecific with the plant species from which the insect was collected. Although the shape and sculpture of pollen from different Myrtaceae species are similar, Myrtaceae pollen could be identified with reasonable certainty based upon the absence of co-flowering myrtaceous species or gross differences in grain size (such as between *Waterhousea floribunda* (F. Muell.) B.Hyland and *Tristaniopsis laurina* (Smith) P.G. Wilson & Waterhouse).

Insect taxa examined were observed to undertake frequent inter-plant movements and relatively long distance inter-plant flights between widely spaced trees. A number of additional large insect taxa, particularly in the Coleoptera (i.e. Tenebrionidae-Alleculinae, Cantharidae, Oedemeridae), occur rarely on mass-flowering subtropical rainforest trees but their inter-plant movements were observed to be far less frequent. Such species could still be important in carrying pollen between flowers in individual inflorescences. Although these relatively sedentary taxa were omitted from consideration they do collect pollen on their bodies thus reducing the pollen available for carriage by insects that undertake more frequent and relatively long distance inter-plant movements.

RESULTS

More than 60,000 insects of all sizes were collected during the three seasons, 1990–1993, in which most of the fieldwork was undertaken. Data on numbers of plant species and individuals sampled, numbers of samples collected, and frequency of large-sized insects within individual samples are given in Williams (1995). Although the number of large insects overall was less than 6 percent the proportion of large insects in individual samples varied from 0–20 percent (Williams 1995). The introduced 'honey bee' *Apis mellifera* frequently represented more than 70 percent of the large-sized insects collected in samples (Williams 1995).

TABLE 1

Pollen loads from large insects (excluding *Apis mellifera*) demonstrating frequent intercanopy movements (approximate pollen grain counts in three abundance classes: 'M' moderate = >100 grains, 'H' heavy = >200 grains, 'A' abundant = >300 grains; total counts given for <100 grains; number of foreign grains given in brackets; '>99' = probably all 'home' pollen with several unassignable grains; '@' = pollen count indeterminate due to grain deformation or similarity of type; 'm' = male, 'f' = female). Site codes: (1) Harrington [31°52'30"S, 152°41'00"E], (2) Manning Point [31°53'30"S, 152°40'00"E], (3) Saltwater Reserve [32°00'30"S, 152°33'45"E], (4) Lansdowne Reserve [31°47'30"S, 152°32'30"E], (5) Lorient Wildlife Refuge [31°45'00"S, 152°32'30"E], (6) Kenwood Wildlife Refuge [31°44'45"S, 152°31'30"E], (7) Wingham [31°52'40"S, 152°22'00"E], (8) Woko National Park [31°49'00"S, 151°47'00"E]. Nomenclature for plants follows Harden (1990–1992)

Insect Taxa	Plant Taxa from which insects were collected	Site	Pollen load	% Home pollen
COLEOPTERA				
Buprestidae				
<i>Castiarina acuminata</i> Kerremans	<i>Alphitonia excelsa</i> (Fenzl) Benth.	1	6	100
<i>C. acuminata</i>	<i>Alphitonia excelsa</i>	1	54(1)	98
<i>C. acuminata</i>	<i>Cuttsia viburnea</i> F. Muell.	5	A	<30
<i>C. acuminata</i>	<i>Guioa semiglauc</i> (F. Muell.) Radlk.	1	M	>95
<i>C. acuminata</i>	<i>Guioa semiglauc</i>	1	A	>99
<i>C. delta</i> Thomson	<i>Tristaniopsis laurina</i> (Smith) P.G.Wilson & Waterhouse	7	A	>99
<i>C. insignis</i> Blackburn	<i>Acmena smithii</i> (Poiret) Merr. & Perry	4	A	100
<i>C. insignis</i>	<i>Tristaniopsis laurina</i>	7	H	>99
<i>C. insignis</i>	<i>Waterhousea floribunda</i> (F. Muell.) B. Hyland	7	A	100
<i>C. neglecta</i> Carter	<i>Alphitonia excelsa</i>	1	M	100
<i>C. neglecta</i>	<i>Alphitonia excelsa</i>	1	M	?100
<i>C. producta</i> Saunders	<i>Acmena smithii</i>	4	A	100
<i>C. producta</i>	<i>Alphitonia excelsa</i>	6	M	unrecorded
<i>C. producta</i>	<i>Guioa semiglauc</i>	1	A	>70
<i>C. producta</i>	<i>Tristaniopsis laurina</i>	5	A	<70
<i>C. producta</i>	<i>Tristaniopsis laurina</i>	7	M	?100
<i>C. producta</i>	<i>Waterhousea floribunda</i>	7	A	100
<i>C. pulchripes</i> Blackburn	<i>Cuttsia viburnea</i>	5	A	>95
<i>C. ?sexcavata</i> Deuquet	<i>Acmena smithii</i> var. <i>minor</i>	8	A	>95
<i>C. ?vicina</i> Saunders	<i>Waterhousea floribunda</i>	7	A	>99
<i>Curis aurifera</i> Castelnau & Gory	<i>Waterhousea floribunda</i>	7	A	>70
<i>C. splendens</i> (Macleay)	<i>Acmena smithii</i> var. <i>minor</i>	8	M	<50
<i>C. splendens</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>Metaxymorpha grayi</i> Parry	<i>Tristaniopsis laurina</i>	5	A	>99
<i>Torresita cuprifera</i> Kirby	<i>Waterhousea floribunda</i>	7	M	>95
Cerambycidae				
<i>Aridaeus thoracicus</i> (Donovan)	<i>Tristaniopsis laurina</i>	5	H	>95
<i>A. thoracicus</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>Distichocera superba</i> (Poll.)	<i>Tristaniopsis laurina</i>	5	H	100
<i>D. superba</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>Hesthesis</i> sp. nr. <i>bizonata</i> Newman	<i>Tristaniopsis laurina</i>	5	M	<30
<i>Tragoceras spencei</i> (Hope)	<i>Waterhousea floribunda</i>	5	A	>90
<i>Tropocalymna dimidiatum</i> (Newman)	<i>Acmena smithii</i>	1	H	>99

Scarabaeidae

<i>Cacachroa gymnopleura</i> (Fischer)	<i>Waterhousea floribunda</i>	5	M	100
<i>Diaphonia dorsalis</i> Donovan	<i>Euroschinus falcata</i> J.D. Hook	3	18(1)	94
<i>D. dorsalis</i>	<i>Waterhousea floribunda</i>	5	A	>99
<i>D. dorsalis</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>Eupoecila australasiae</i> (Donovan)	<i>Alphitonia excelsa</i>	1	M	100
<i>E. australasiae</i>	<i>Waterhousea floribunda</i>	5	A	>99
<i>E. australasiae</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>Glycyphana brunnipes</i> (Kirby)	<i>Alphitonia excelsa</i>	6	M	<70
<i>G. brunnipes</i>	<i>Euroschinua falcata</i>	3	21(7)	33
<i>G. brunnipes</i>	<i>Tristaniopsis laurina</i>	5	M	>99
<i>Polystigma punctatum</i> (Donovan)	<i>Alphitonia excelsa</i>	1	H	>99
<i>P. punctatum</i>	<i>Tristaniopsis laurina</i>	5	A	>95
<i>P. punctatum</i>	<i>Waterhousea floribunda</i>	7	A	>99
<i>P. punctatum</i>	<i>Waterhousea floribunda</i>	5	A	>95

DIPTERA**Calliphoridae**

<i>Paramenia</i> sp.	<i>Alphitonia excelsa</i>	1	H	>90
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Nemestrinidae

<i>Austrogastromyia nigrovittata</i> Mackerras	<i>Cuttsia viburnea</i>	5	A	100
<i>A. ?punctata</i> Macquart	<i>Waterhousea floribunda</i>	7	H	>95

Syrphidae

<i>Dideopsis</i> sp.	<i>Alphitonia excelsa</i>	1	3	100
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Tabanidae

<i>Cydistomyia nigripicta</i> (Macquart)	<i>Tristaniopsis laurina</i>	7	9(1)	89
<i>Scaptia auriflua</i> Donovan	<i>Waterhousea floribunda</i>	5	M	>95
<i>S. ?quadrimacula</i> Walker	<i>Cuttsia viburnea</i>	5	H	>95

HYMENOPTERA**Ichneumonidae**

<i>Echthromorpha intricatoria</i> (Fabricius)	<i>Alphitonia excelsa</i>	1	H	100
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Pompilidae

<i>Chryptocheilus</i> sp.	<i>Tristaniopsis laurina</i>	7	A	100
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Scoliidae

<i>Campsomeris ?tasmaniensis</i> (Saussure)	<i>Alphitonia excelsa</i>	1	83(3)	96
<i>C. ?tasmaniensis</i>	<i>Diospyros australis</i> (R. Br.) Hiern	5	A	<1
<i>C. zonata</i> Smith	<i>Tristaniopsis laurina</i>	5	A	>99
<i>Scolia verticollis</i> (Fabricius)	<i>Alphitonia excelsa</i>	1	H	>95
<i>S. ?verticollis</i>	<i>Tristaniopsis laurina</i>	7	M	>95
<i>Scolia</i> sp.	<i>Tristaniopsis laurina</i>	7	M	>95

Sphecidae

<i>Bembicinus</i> sp.	<i>Alphitonia excelsa</i>	1	3(1)	66
<i>Bembix promontorii</i> Lohrman	<i>Alphitonia excelsa</i>	1	4	100
<i>Bembix</i> sp. 1	<i>Alphitonia excelsa</i>	1	8(@4)	@50

<i>Bembix</i> sp. 2	<i>Acmena smithii</i>	2	19(8)	58
<i>Sceliphron laetum</i> (Smith)	<i>Tristaniopsis laurina</i>	7	M	>90
<i>Sphex ephippium</i> Smith	<i>Alphitonia excelsa</i>	1	7(4)	43
<i>S. fumipennis</i> Smith	<i>Alphitonia excelsa</i>	1	48(3)	94
<i>Tachysphex</i> sp.	<i>Alphitonia excelsa</i>	1	96(0)	100
Tiphiidae				
<i>Anthobosca</i> ? <i>signata</i> Smith	<i>Alphitonia excelsa</i>	1	M	>95
<i>A. ?signata</i>	<i>Alphitonia excelsa</i>	1	A	100
<i>A. ?signata</i>	<i>Tristaniopsis laurina</i>	5	M	>95
<i>Diamma bicolor</i> Westwood	<i>Alphitonia excelsa</i>	1	73(7)	>90
<i>Dimorphothynnus dimidiatus</i> (Smith)	<i>Acmena smithii</i>	2	H	>95
<i>D. dimidiatus</i>	<i>Acmena smithii</i>	1	83(@50)	<40
<i>D. dimidiatus</i>	<i>Guioa semiglauc</i>	1	M	100
<i>Hemithynnus apterus</i> (Oliver)	<i>Acmena smithii</i>	2	22(?)	>50
<i>H. rufiventris</i> (Guerin)	<i>Tristaniopsis laurina</i>	5	H	>99
<i>Rhagigaster</i> sp. nr. <i>klandensis</i> Guerin	<i>Alphitonia excelsa</i>	1		?home
<i>Zaspilothynnus</i> sp. nr. <i>campanularis</i> (Smith)	<i>Alphitonia excelsa</i>	1	38(@9)	@76
Vespidae				
<i>Abispa splendida</i> (Guerin)	<i>Tristaniopsis laurina</i>	7	A	>99
<i>Bidentodynerus bicolor</i> (Saussure)	<i>Tristaniopsis laurina</i>	7	H	80
? <i>Epidodynerus</i> sp.	<i>Tristaniopsis laurina</i>	5	M	<60
<i>Polistes humilis</i> (Fabricius)	<i>Alectryon coriaceus</i>	2	8(3)	63
<i>P. tepidus</i> (Fabricius)	<i>Alphitonia excelsa</i>	1	M	100
<i>Pseudabispa confusa</i> van der Vecht	<i>Tristaniopsis laurina</i>	7	A	>99

Pollen loads from 86 individual insects, comprising approximately 60 native insect species in 13 families, were examined (Table 1). Although this number is a small proportion of the large insects the sample represented nearly all of the larger-sized native species and genera collected during the pollination study, and in most instances represented all of the individuals collected for individual taxa. None of the species or genera examined were considered to be specialist foragers as all species occurred either in several habitats or upon a variety of plant species (Williams 1995), or carried mixed pollen loads (Table 1) indicating that foraging patterns are generalised. However, the pollen loads of some taxa indicated temporal fidelity or constancy to the host plant. Although numerous individuals and taxa were observed at close range in the field, very few large insects exhibited cleaning behaviour (which would have reduced their pollen load).

Coleoptera-Buprestidae

The buprestid fauna collected from the lower Manning includes genera that are phyllophagous or, alternatively, floricolous as adults (Williams 1995). The principal floricolous genus collected was *Castiarina* (sensu Gardner 1989) (Table 1), but species of *Torresita*, *Curis*, *Metaxymorpha*, *Calodema* and *Neocuris* also occurred on flowers of rainforest trees. *Neocuris* was excluded from the genera examined for pollen loads, due to the small size of individuals (<5 mm), and although *Calodema* was observed on *Cuttsia viburnea* we were unable to collect specimens due to the difficulty of hand netting in the canopy.



Figure 1. Mixed pollen load on the hypomeron of *Castiarina acuminata* (Buprestidae). Note almost total absence of surface sculpture at this point (scale = 100 μ m).

Fifteen (60%) of the 25 Buprestidae examined had abundant pollen loads (Table 1). *Castiarina* spp. generally carried large pollen loads composed primarily of 'home' pollen. In 2 specimens of *Castiarina acuminata* Kerremans collected on *Alphitonia excelsa*, in littoral rainforest at Harrington, pollen loads were light (6–53 grains), although principally consisting of 'home' pollen. On *C. neglecta* Carter, however, loads of *Alphitonia excelsa* pollen from the same site were more substantial (M). Species collected on myrtaceous blossoms (*Acmena smithii* (Poir.) Merr. & Perry, *Tristaniopsis laurina*, *Waterhousea floribunda*) generally carried heavy to abundant pollen loads which were almost exclusively 'home' pollen. Pollen loads on *Curis* spp. collected from Myrtaceae were more variable (M-A, i.e. less than 50 to more than 90% 'home' pollen).

Although vestiture in several non-Australian buprestid genera is long and dense (e.g., *Acmaeodera*, *Julodis*) most Buprestidae possess short setae.

Placement of pollen was principally ventral and on anterodorsal areas. Major sites of pollen deposition were the frontal cavity of the head, thoracic hypomera (Fig. 1), prosternum and metasternum, and antennal and coxal cavities.

Surface punctation and vestiture on the head, pronotum and anteroventral surfaces generally, permitted the retention and transport of potentially large pollen loads (Table 1). Vestiture on the abdominal ventrites and sutures between individual abdominal segments carried significant loads. Vestiture is vulnerable to wear and abrasion which may reduce pollen carrying capacity.

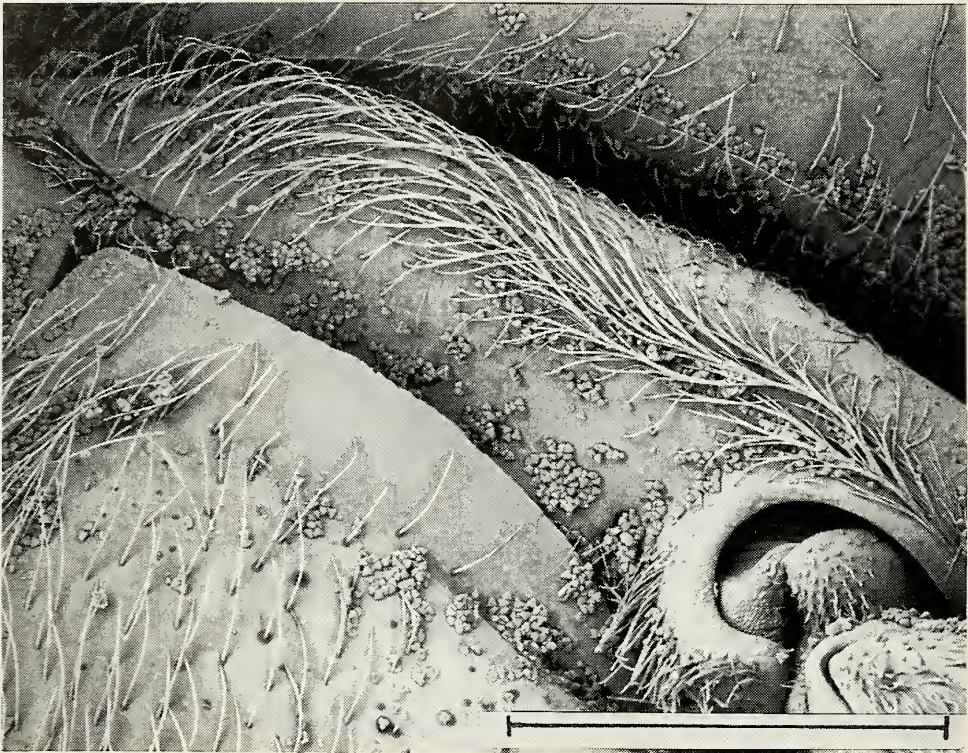


Figure 2. Pollen grains associated with the metacoxal region, *Stenoderus* sp. (Cerambycidae). Note general absence of integument sculpture or punctation at this magnification (scale = 500 μ m).

Coleoptera–Cerambycidae

Although Cerambycidae are a taxonomically diverse group within the rainforest Coleoptera, most regionally-occurring species are phyllophagous (Williams 1995).

Large Cerambycidae are infrequent or spatially and temporally localised flower visitors in rainforest. Of the 5 large species collected at blossoms, only *Tropocalymma dimidiatum* (Newman) and *Distichocera superba* (Poll.), are known to be regionally restricted to rainforest (G. Williams unpublished data). Although widely distributed in coastal habitats (Webb 1987, G. Williams pers. obs.) *Aridaeus thoracicus* (Donovan) was collected only on *Tristaniopsis laurina* and *Waterhousea floribunda* at Wingham during this study.

Three (43%) of the Cerambycidae carried abundant pollen loads. Both *D. superba* and *T. dimidiatum* carried heavy or abundant pollen loads which were composed almost totally of 'home' pollen. *Aridaeus thoracicus* (H-A: more than 95 to more than 99% 'home' pollen) and *Tragocerus spencei* Hope (A; >90%) carried heavy pollen loads but the pollen load carried by *Hesthesis* sp. near *bizonata* Newman was smaller (M) and contained a high proportion of foreign pollen (<30% home pollen).

Principal placement of pollen in Cerambycidae was on the ventral and anterodorsal regions. The regions of the head, antennal and coxal cavities (Fig. 2), and mesosternum were major deposition sites. In Cerambycidae, however, the prosternum is generally reduced to a smooth convex structure, without a prominent frontal lobe or vestiture, and this reduces its capacity to function as a pollen deposition site.

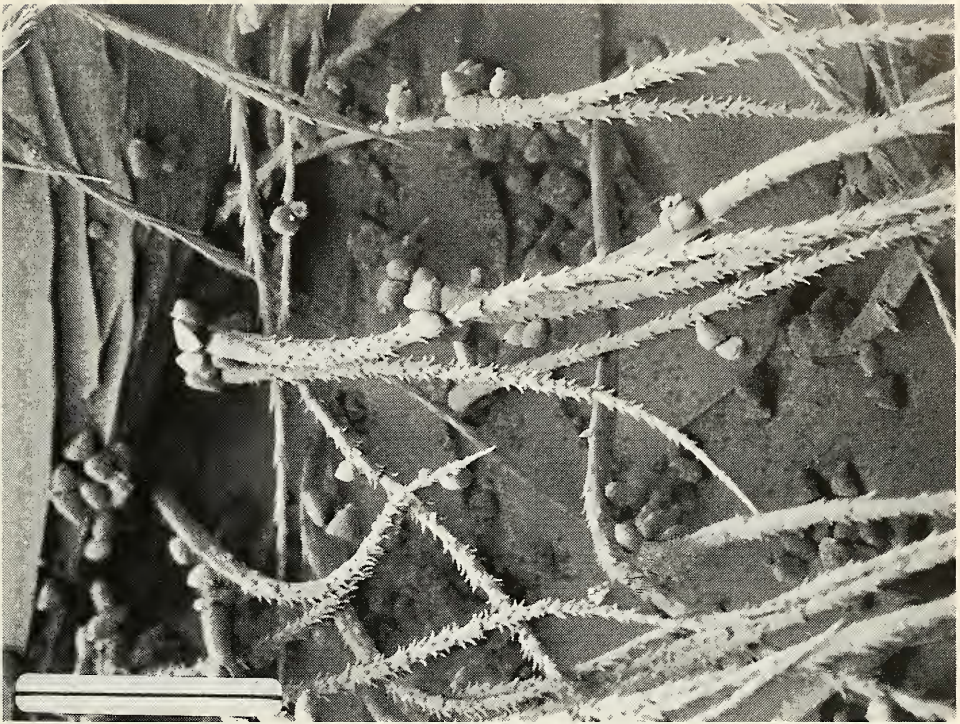


Figure 3. *Cacochroa gymnopleura* (Cetoniinae), lateral detail of hooked palynophilic setae, and pollen grains, in the vicinity of the hypomeron. Similarly hooked setae are recorded in Apoidea (see Barth [1991], plate 13) and Syrphidae (Holloway [1976], figure 8) (scale 100 μ m).

Coleoptera–Scarabaeidae–Cetoniinae

Adult Scarabaeidae–Cetoniinae constitute a flower-adapted group within the otherwise predominantly phyllophagous Scarabaeidae (Lawrence and Britton 1994, Williams 1995). Cetoniinae collected comprised 5 genera, each represented by a single species.

Seven (50%) Cetoniinae carried abundant quantities of pollen. *Diaphonia dorsalis* Donovan carried variable quantities of pollen (17 to >300 grains) and this was almost exclusively 'home' pollen. *Cacochroa gymnopleura* (Fischer) carried abundant quantities of 'home' pollen only, but is a common species widely encountered on the flowers of Myrtaceae–Leptospermoideae (Webb 1987) in eastern Australia. Similarly, *Eupoecila australasiae* (Donovan) (M–A: >99%) and *Polystigma punctatum* (Donovan) (H–A: >95%) carried high 'home' pollen loads and are both widely encountered in coastal sclerophyll forests. *Glycyphana brunnipes* (Kirby) carried smaller variable loads (21 to >100: >60 to >99%). Although common on *Euroschinus falcata* J.D.Hook. (Anacardiaceae), at Saltwater, pollen loads were very low (Table 1) or could not be readily discerned under the microscope.

Although Cetoniinae generally lack the prominent integumental punctation of Buprestidae they possess long, dense setal clusters and surface vestiture which readily ensnare pollen grains (Fig. 3) (Crowson 1981).

Hooked setae were recorded on the lateroventral surface of *Cacochroa gymnopleura* (Fig. 3) during scanning electron microscopy investigation of pollen lodgement. Englund (1993) has recorded branched setae on the European cetoniine *Cetonia aurata* (L.) but

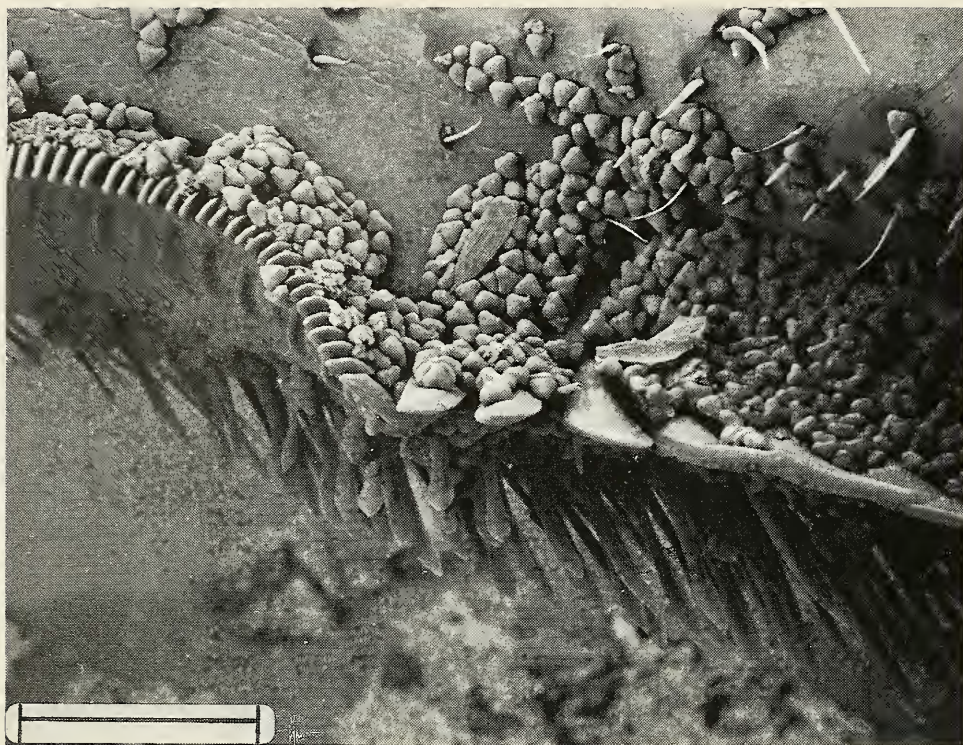


Figure 4. *Anthobosca ?signata* (Tiphidae); detail of specialised 'pollen comb' on the first tarsomere (scale = 100 μ m).

these structures have not otherwise been reported from the Cetoniinae. Crowson (1981) noted modified, plumose, hairs in the scarabaeoid genus *Amphicoma* (Glaphyridae) and hooked setae similar to those in *C. gymnopleura* have been found on the glaphyrid genus *Lichnanthe* (J.F. Lawrence pers. comm.). Hooked setae may occur more widely in pollen-feeding scarabaeoids but can be readily overlooked under normal magnification (J.F. Lawrence pers. comm.). Similarly shaped setae have been described and figured from specialised Apoidea and Syrphidae (Diptera) (Holloway 1976, Barth 1991).

The head, and lateral and ventral surfaces of the prothorax of Cetoniinae carry heavier pollen loads than other regions of the body. Unlike Buprestidae, the frons does not generally possess a pronounced frontal or vertical cavity or depression and pollen clusters are not normally associated with the frons. The clypeus however, frequently possesses large, readily discernable pollen loads. The importance of the clypeus as a site of pollen deposition probably reflects the pronounced development of this structure in Scarabaeidae generally (Carne 1957a, 1958, Britton 1970, Matthews 1972, Crowson 1981, Lawrence and Britton 1991), although some Dynastinae and Rutelinae possess a reduced clypeus (Carne 1957b, 1958).

Coleoptera potentially carry large pollen loads (54% of specimens cited in Table 1 carried abundant quantities of pollen). Feeding behaviour in anthophilous Buprestidae, Cerambycidae and Cetoniinae is similar. Species characteristically feed on nectar by inserting the head and mouthparts into the perianth or hypanthium. Short distance, inter-flower movements are undertaken without the aid of flight, by 'clambering' across and through paniculate and corymbose inflorescences. Long distance, inter-plant flights are

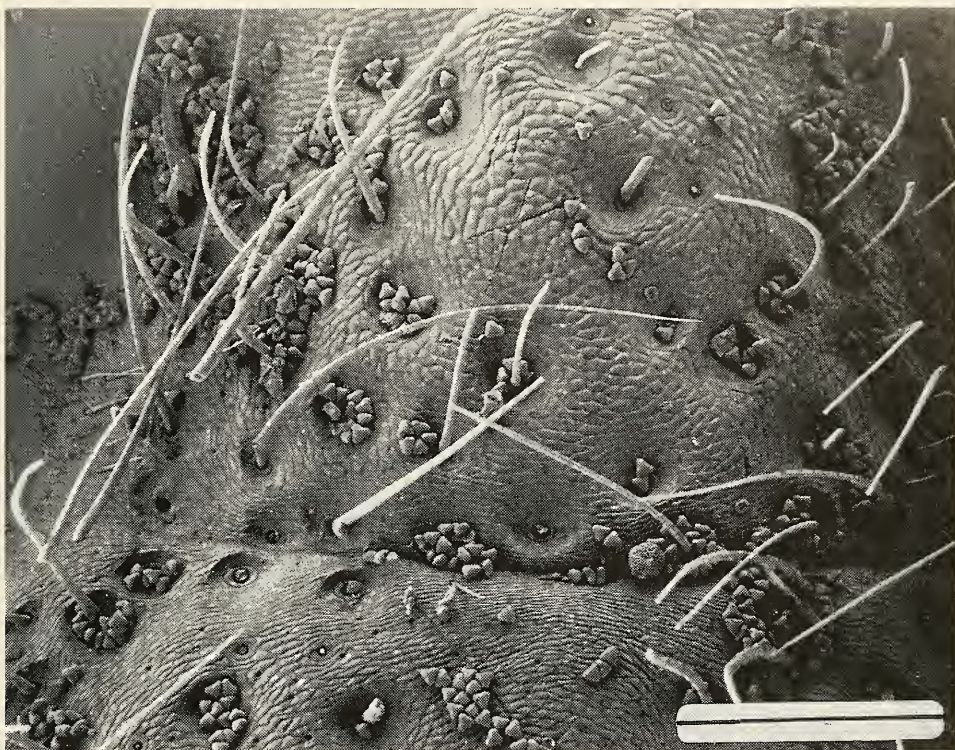


Figure 5. Pollen clusters (principally Myrtaceae) in fascial punctation, *Scolia* sp. (Scoliidae) (scale = 200 μ m).

undertaken either without preceding visual warning, as in Cetoniinae, or as a response to disturbance (e.g., Buprestidae-*Castiarina*). The similarities in sites of pollen deposition on these taxonomically unrelated families is not unexpected given their generally similar foraging behaviour.

Hymenoptera (Ichneumonoidea, Sphecoidea, Vespoidea)

Pollen was found on members of the families Tiphidae, Scoliidae, Sphecidae, Pompilidae and Vespidae (aculeate wasps), and Ichneumonidae. The Tiphidae (6 genera, 7 spp.), Sphecidae (5 genera, 8 spp.) and Vespidae (5 genera, 6 spp.) were the most abundant larger-sized wasps frequently carrying significant (>100 grains) pollen loads. Only 18 per cent of larger-sized wasps carried abundant pollen loads. This was lower than the 54 per cent ($n=46$) of Coleoptera individuals that carried abundant quantities of pollen (Table 1).

Most wasp records were from *Tristaniopsis laurina* (Myrtaceae) and *Alphitonia excelsa* (Williams and Adam 1995). While Tiphidae were generally common on *A. excelsa*, they exhibited variation in pollen loads (1 to >300 grains) and percentage of 'home' pollen (0–100%) carried. This variation in pollen loads did not correlate with size of individual taxa.

Variation in number of pollen grains and percent 'home' pollen was found in all families. Hymenoptera collected from *Tristaniopsis laurina*, at the Lorient study site in wet sclerophyll forest, and at the Wingham site in rainforest carried generally greater pollen loads (range Lorient M-A; Wingham M-A) and loads dominated by 'home' pollen

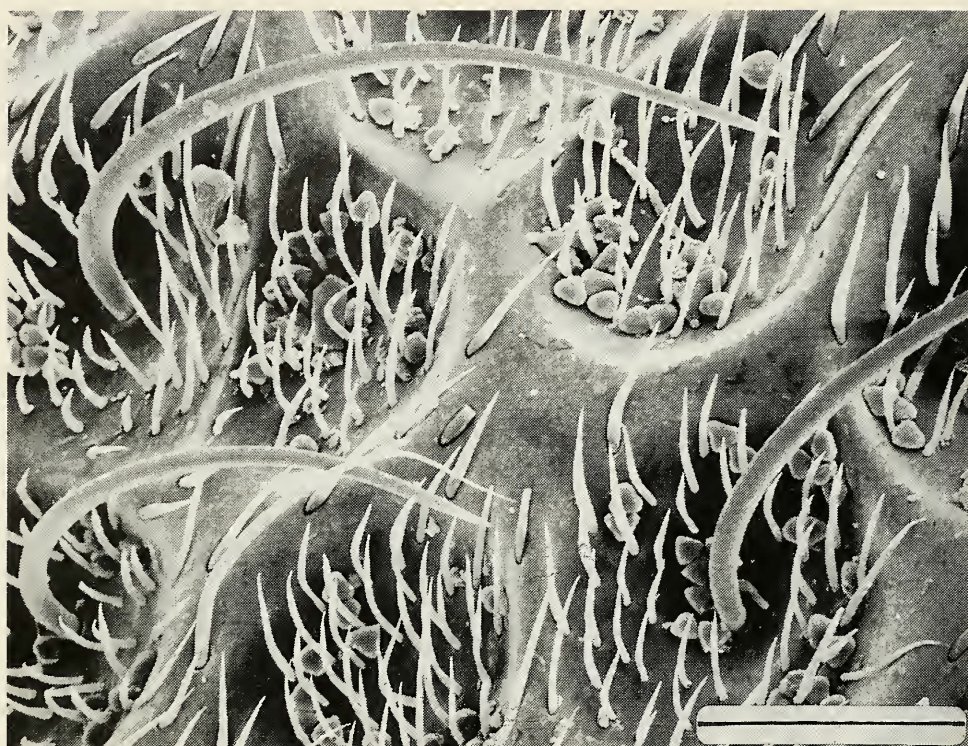


Figure 6. Detail of pollen, in lateral thoracic punctation, *Abispa* sp. (Vespidae) (scale = 100 μ m).

(range Loric less than 60 to more than 99%; Wingham 80 to more than 99%) (Table 1). In part, this is related to the relatively greater amounts of pollen available from *T. laurina* flowers (Williams 1995).

Sites of pollen deposition on large wasps were more varied than on Coleoptera (see Figs. 4, 5, 6). The head, basal antennomeres and dorsum of the mesosoma are major pollen deposition sites (the metasoma was found to carry little pollen except in the eumene *Bidentodynerus bicolor* (Saussure)). The legs, particularly the femora and tibiae, carry pollen loads to an extent not generally paralleled in the Coleoptera. In *Anthobosca ?signata* Smith (Tiphidae) there are specialised 'pollen combs' on the first tarsomere (Fig. 4) and these carried the largest proportion of the pollen load (functionally analogous structures are found in Apoidea and floricolous Scarabaeidae [Crowson 1981, Roubik 1989]). In *Dimorphothynnus dimidiatus* (Smith) (Tiphidae) pollen was associated with mesepisternal grooves. In *Sphex fumipennis* Smith, *S. ephippium* Smith and *Bembicinus* sp. (Sphecidae), *Campsomeris ?tasmaniensis* (Saussure) (Scoliidae), *Rhagigaster* sp. near *kiandrensis* Guerin and *Zelebora xanthorrhoei* (Smith) (Tiphidae-Thynninae) the base of the forewings was the site of pollen deposition. In *Echthromorpha intricatoria* (Fabricius) (Ichneumonidae) pollen was deposited on the prementum, and malar region of the head, and was associated with the forelegs.

Robust, setose Hymenoptera-Scoliidae, and some Vespidae-Eumeninae, move across and between inflorescences in a similar manner to that of large Coleoptera. This 'clambering' method of inter-flower movement maximises physical contact between the flower and insect integument and consequently heavy pollen loads are carried, deposited widely upon the insect (Appendix).

Sphecidae undertake frequent inter-plant and inter-flower movements and remain on individual inflorescences or flowers for short periods (usually <10 seconds). For example, *Bembix* spp. generally made foraging bouts of less than 3 seconds at individual flowers. In addition, sphecsids frequently feed by having their body relatively raised above most of the flower structure and this reduces contact with stamens. Although closely related to Apoidea (Naumann *et al.* 1991) sphecid behaviour differed from that of bees, which generally undertook foraging bouts involving prolonged and repeated contact with stamens. Sphecsids visited only a small number of the plant species sampled. They were most frequently found on *Alphitonia excelsa*, which releases little pollen unless the petals (which initially encapsulate the stamens) are firmly depressed (Williams 1995) — which Sphecidae generally do not achieve due to light body weight and feeding posture upon blossoms.

There is no obvious explanation for the generally small pollen loads on Tiphiidae, which foraged in a similar manner to that of Scoliidae and Vespidae. These are principally slender species, exceptions being *Anthobosca ?signata* (which superficially resembles a large scoliid), and *Hemithynnus apterus* (Oliver), *H. rufiventris* (Guerin) and *Zaspilothynnus* sp. near *campanularis* (Smith). The latter 3 species however, appeared to be uncommon and were rarely collected.

Diptera

Although small-sized Diptera (<6 mm) are a very abundant component of the insect fauna visiting subtropical rainforest flowers (Williams 1995) very few large species were observed or collected. The pool of larger-sized Diptera in subtropical rainforests, from which pollinators can be drawn, appears to be small. However, entomophilous rainforest trees flowering on rainforest margins are able to recruit large anthophilous flies, such as Bombyliidae, from adjoining vegetation types.

Syrphidae are generally considered to be variously specialised oligolectic flower visitors (Holloway 1976, Faegri and van der Pijl 1979, Colless and McAlpine 1991). Few ecologically specialised Syrphidae were collected from tree blossoms (see Williams 1995) but several generalist semi-adapted genera occurred (i.e. *Psilota*, *Eristalinus*, 'Eristalis', *Helophilus*). The single syrphid examined, *Dideopsis* sp., carried few pollen grains.

The genus *Austrogastromyia* (Nemestrinidae) occurred at particular times on only two plant species (*Cuttsia viburnea* F. Muell. — Escalloniaceae, *Waterhousea floribunda* — Myrtaceae) but carried heavy and abundant pollen loads, with minimal content (<5 to 0%) of foreign pollen. Similarly, *Paramenia* sp. (Calliphoridae) carried heavy pollen loads (>90% home pollen). Pollen loads carried by *Scaptia* spp. (Tabanidae) ranged from M-H, with >95% home pollen. The tabanid *Cydistomyia nigripicta* Macquart, however, carried minimal loads (<10 grains) even though foraging upon mass-flowering *Tristaniopsis laurina*.

The anteroventral surface generally, and the head, femora and tibiae were the major deposition sites. In *Austrogastromyia nigrovittata* Mackerras the abdominal sternites, and in both *A. nigrovittata* and *A. ?punctata* Macquart, lateral prothoracic sclerites (i.e., anepisternite, sternopleura), carried pollen masses. In general, however, the dense, pilose surface of large Diptera precluded pollen accretion on the surface of the integument.

DISCUSSION

This study has shown that although large insects comprise only a small proportion of the insect visitors to subtropical rainforest flowers they are capable of transporting large quantities of pollen. More detailed studies of long distance movements by these insects, and of their effectiveness as pollinators, are required to assess the importance of large insects to the reproductive ecology of subtropical rainforest plants.

Large insects collected from Myrtaceae generally carried heavy pollen loads which consisted principally of 'home' pollen and the examination of pollen loads on insects generally indicated temporal foraging constancy by individual taxa, which would minimise pollen loss to non-conspecific flowering plants. Sites of pollen deposition on the integument of individual insect taxa were diverse and pollen loads were variable but are influenced by time spent foraging, foraging behaviour, body morphology and size of the insect, as well as quantity of pollen presented by individual flowers and plants (Williams 1995). For example, the relatively small amounts of pollen produced individually by the flowers of *Alphitonia excelsa* (Fenzl) Benth. (Rhamnaceae), and the method of pollen presentation which requires depression of the stamens and enveloping petals to release pollen masses (Williams 1995), may restrict the pollen loads found on anthophilous insects regardless of the time they individually spend foraging and the number of flowers visited. In general Coleoptera carried large amounts of pollen contrary to the suggestion that pollen does not adhere to their 'smooth' bodies (e.g., Percival 1965, Archibold 1995). It has been suggested that large Coleoptera are pollinators of trees and shrubs in a number of Australian open forest and woodland communities (e.g., Hawkeswood 1980, 1981, 1982, Webb 1986, 1987). Our results suggest this may also be true in rainforests.

Based upon the development of body vestiture, two broad groupings of taxonomically unrelated anthophilous insects on mass-flowering rainforest plants can be recognized:

1. species with sparse or poorly developed vestiture (e.g., Buprestidae, Cerambycidae, Vespidae) which generally spend individually long periods foraging on inflorescences and make inter-flower movements upon individual trees by clambering from blossom to blossom. In so doing large quantities of pollen may adhere to the body integument;
2. species with dense, often long, setae (e.g., Sphecidae, some Diptera) that are unlikely to carry heavy pollen loads directly on the integument. Rather, individual pollen grains are ensnared by setae, or small pollen clusters may aggregate in spatially discrete regions. Whilst this latter group contains species characteristically considered specialised in their foraging behaviour these generally transport small pollen loads potentially resulting in reduced contributions to reproductive success in mass-flowering rainforest plants.

The flowers of most subtropical rainforest trees conform to the entomophilous floral syndrome (Williams and Adam 1994). Birds and bats are important inter-plant and long-distance pollinators in many ecosystems but are relatively rare visitors to plants with entomophilous flowers in New South Wales subtropical rainforests (Williams 1995). Consequently, larger-sized insects that have a propensity to undertake flights to widely-separated flowering plants (even though their movements may be short compared with that of many birds and bats) may be important in the reproductive ecology of fragmented rainforest plant populations because isolated plants can suffer greatly reduced levels of pollination.

The daily movements by small insects (<6 mm), particularly those of small Coleoptera and brachyceran Diptera, in subtropical rainforests are predominantly within the crowns of individual trees, with the majority of inter-plant movements being to near-neighbours (G. Williams pers. obs). As such they are likely to promote autogamous and geitonogamous pollination in self-compatible species. The larger insects included in this study undertook frequent daily movements between trees. Such inter-plant movements are important for self-incompatible and dioecious plant species and promote out-crossing, rather than geitonogamous pollination.

Even if inter-plant movements occur at low frequency these can be sufficient to result in successful pollination of highly dispersed plants (Frankie, Opler and Bawa 1976, Englund 1993).

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APPENDIX

Primary Pollen Deposition Sites. (H) head, (T) thorax (incl. wings in Diptera and Hymenoptera), (L) legs, (A) abdomen (in Coleoptera the elytra, for purposes of pollen deposition function as part of the abdomen).

COLEOPTERA**Buprestidae**

Castiarina acuminata (H) frontal cavity, vertex; (T) mesosternum, coxal cavities, prosternum, metacoxal plate, pronotal hypomera; (L) procoxae, femora; (A) elytral striae, ventrites.

Castiarina delta (T) pronotal foveae, hypomera, metacoxal plate; (A) elytral striae, elytra generally.

Castiarina insignis (H) antennal cavities, frontal cavity; (T) prosternum, mesosternum, metacoxal cavities, metacoxal plate; (L) coxae; (A) abdominal ventrite 1, apical ventrite, anterolateral elytral margins.

Castiarina neglecta (H) antennal cavities, anterior margin of eye; (T) coxal cavities, pronotal hypomera, mesosternum.

Castiarina producta (H) antennal cavities, frons, genae; (T) prosternal lobe, pronotal hypomera, mesosternum, coxal cavities, metacoxal plate; (L) coxae; (A) ventral surface generally.

Castiarina pulchripes (H) vertical suture; (T) prosternum, prosternal and metasternal lobes, mesosternum, coxal cavities; (L) profemora.

Castiarina ?sexcavata (H) antennal cavities, vertical suture; (T) prosternal lobe, metacoxal plates, ventral surface generally; (A) ventral surface generally.

Castiarina ?vicina (T) anterior and basal pronotal margins, prosternal and metasternal lobes, ventral surface; (L) metafemora; (A) elytral striae, ventral surface generally.

Curis aurifera (H) basal margin, frontal cavity; (T) pronotal fossae, ventral surface generally; (A) ventral surface generally.

Curis splendens (H) frontal cavity; (T) dorsal and ventral punctation generally, lateral pronotal margins, coxal cavities, metacoxal plate, ventral surface generally; (A) dorsal and ventral punctation generally, ventral surface generally, epipleurae.

Metaxymorpha grayi (H) antennal cavities, scape, frons, mentum, gula; (T) prosternum, metasternum, coxal cavities; (A) epipleurae.

Torresita cuprifera (H) antennal cavities; (T) pronotum, punctation of ventral surface; (A) punctation of ventral surface.

Cerambycidae

Aridaeus thoracicus (H) antennomeres 1–4, vertex; (T) meso-metepisterna, mesosternum, mesocoxal cavities, ventral surface generally; (L) mesocoxae, basal 1/2 femora; (A) elytral humeri.

Distichocera superba (H) antennal cavities, scape, antennae generally, genae, vertical and frontal cavities; (T) mesosternum, coxal cavities, ventral surface generally; (L) coxae; (A) humeral calli, epipleurae, ventral surface generally.

Hesthesis sp.nr. *bizonata* (T) mesosternum, mesosternal cavities; (L) mesocoxae.

Tragocerus spencei (H) frons, vertex; (T) pronotum, metasternum.

Tropocalymna dimidiatum (H) frontal cavity, gulae; (T) mesocoxal cavity, metacoxal cavity and plate; (L) metacoxae.

Scarabaeidae-Cetoniinae

Cacachroa gymnopleura (H) head generally; (T) dorsal and ventral surface generally; (L) femora, tibiae generally; (A) elytra and ventral surface generally.

Diaphonia dorsalis (H) antennal cavities, anterior ocular margin, ocular canthi, genae, mentum; (T) prosternal lobe, ventral surface generally; (L) protibiae; (A) ventral surface generally, epipleurae.

Eupoecila australasiae (H) clypeus, antennal cavities; (T) anterolateral pronotal angles, prosternum, metasternal lobe, ventral surface generally; (L) profemora; (A) elytral base laterad of humeri, ventral surface generally.

Glycyphana brunnipes (H) clypeus, antennal cavities; (T) anterolateral pronotal angles, pronotal hypomera, coxal cavities, metacoxal plate, meso-metasterna, ventral surface generally; (L) coxae; (A) basal margin of elytra, epipleurae.

Polystigma punctatum (H) clypeus, antennal cavities, genae, labial palps; (T) lateral margins of pronotum, pronotal hypomera, ventral surface generally; (L) femora, protibiae; (A) sutures of abdominal ventrites, ventral surface generally.

DIPTERA**Calliphoridae**

Paramenia sp. (L) base of protibiae, apex of profemora.

Nemestrinidae

Austrogastromyia nigrovittata (H) prementum, ocular margins, head generally; (T) sternopleura, anepisternites; (L) pro-meso femora and tibiae; (A) abdomen generally.

Austrogastromyia ?punctata (H) frons; (T) anepisternites, anteroventral surface, base of ventral wing surface (L) legs generally.

Syrphidae

Dideopsis sp. (H) head generally.

Tabanidae

Cydistomyia nigripicta (T) thorax generally.

Scaptia auriflua (H) eyes, head generally; (T) ventral surface generally.

Scaptia ?quadrinacula (H) head generally; (T) dorsal and ventral surfaces generally; (L) femorae, tibiae.

HYMENOPTERA**Ichneumonidae**

Echthromorpha intricatoria (H) prementum, malar region; (L) procoxae, basal 1/2 profemora.

Pompilidae

Chryptocheilus sp. (H) basal margin; (T) pronotum, mesepimeron, mesonotum, propleuron; (L) trochanter.

Scoliidae

Campsomeris ?tasmaniensis (**H**) mandibles, clypeus, head generally, including antennomeres; (**T**) thorax generally, incl. wing bases; (**L**) femora, tibiae, legs generally; (**A**) gaster generally.

Campsomeris zonata (**H**) head generally; (**T**) ventral surface generally; (**L**) pro-mesofemora.

Scolia verticollis (**H**) mandibles, frons, clypeus; (**T**) thorax generally; (**L**) protarsomeres.

Scolia ?verticollis (**H**) basal antennal segments, vertex; (**T**) anterior pronotal margin; (**L**) pro-mesocoxae, femora, tibiae.

Scolia sp. (**H**) distal margin; (**T**) anterior pronotal margin, anteroventral surface.

Sphécidae

Bembicinus sp. (**H**) antennal cavities; (**T**) base of forewings; (**L**) profemora.

Bembix promontorii (**H**) vertex; (**T**) base of mesosoma.

Bembix sp. 1 (**H**) basal margin; (**T**) dorsal surface generally.

Bembix sp. 2 (**H**) head generally; (**T**) dorsal surface generally.

Sceliphron laetum (**T**) anteroventral surface generally.

Sphex ephippium (**H**) head generally; (**T**) thorax generally, base of wings.

Sphex fumipennis (**T**) lateral thoracic region generally, base of forewings; (**L**) trochanters.

Tachysphex sp. (**H**) mandibles, prementum.

Tiphiidae

Anthobosca ?signata (**H**) scape, frons, clypeus, head generally; (**L**) specialized 'combs' on prolegs, tibiae, metafemora.

Dianma bicolor (male) (**T**) lateral margin of prothorax; (**L**) profemora.

Dimorphothynnus dimidiatus (**H**) antennal cavities, frons, clypeus, vertex; (**T**) mesoscutum, mesepisternal grooves (ant. margin); (**L**) prolegs generally.

Hemithynnus apterus (**H**) vertex; (**T**) pronotum, mesoscutum, ventral surface generally.

Hemithynnus rufiventris (**H**) basal antennomeres, vertex, head generally; (**T**) lateral and ventral surface of mesosoma.

Rhagigaster sp. nr. *kiandrensis* (**T**) propodeum, base of forewings.

Zaspilothynnus sp. nr. *campanularis* (**T**) lateral margins of mesosoma, especially sutures, propodeum; (**A**) base of gaster.

Zebleboria xanthorrhoei (**H**) scape, frons, antennal cavities; (**T**) base of forewings.

Vespidae

Abispa splendida (**T**) ventral surface generally; (**L**) coxae, pro-mesofemora.

Bidentodynerus bicolor (**H**) head; (**T**) mesepisternum; (**A**) base of petiole, gaster.

?Epidodynerus sp. (**H**) antennal cavities, clypeus; (**T**) ventral surface generally.

Polistes humilis (**L**) protarsomeres.

Polistes tepidus (**H**) antennal cavities; (**T**) ventral surface of mesosoma generally; (**L**) prolegs generally.

Pseudabispa confusa (**H**) antennal cavities; (**T**) mesopleura.